Time and energy budgets of Oystercatchers Haematopus ostralegus occupying territories of different quality

Kersten, M.

Published in:
Ardea

TIME AND ENERGY BUDGETS OF OYSTERCATCHERS *HAEMATOPUS OSTRALEGUS* OCCUPYING TERRITORIES OF DIFFERENT QUALITY

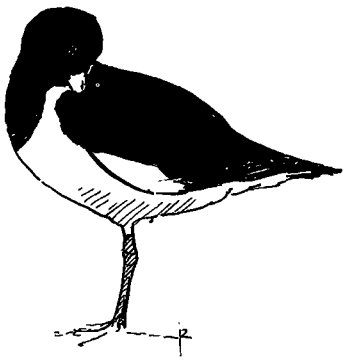
MARCEL KERSTEN

Kersten M. 1996. Time and energy budgets of Oystercatchers *Haematopus ostralegus* occupying territories of different quality. Ardea 84A: 291-310.

The effect of territory quality on the time and energy allocation of Oystercatchers was investigated on the island of Schiermonnikoog in the Dutch part of the Wadden Sea. Low quality leapfrog territories required a higher level of parental effort for successful reproduction than high quality resident territories. The time budgets of residents and leapfrogs differed slightly, the main difference occurring during the chick-rearing stage when leapfrogs spent on average 8.2% of the time available during low water in flight in order to transport food to the chicks, compared to only 2.9% in residents.
In both residents and leapfrogs, inactivity (including preening) constituted a considerable part of the time budget, comprising almost 50% of the low water period during the pre-laying stage and decreasing to 23% during the incubation stage when each bird spent almost half the time on the clutch. Analysis of individual time budgets during the incubation stage revealed that time spent inactive must be considered 'surplus time' since this can be reallocated to foraging when the proportion of time devoted to incubation increased. Obligatory inactivity required less than 10% of the time available during low water. The persistence of 'surplus' time during the chick-rearing stage suggests that parental effort is not constrained by a shortage of time.
Energy expenditure, estimated from time-budgets, agreed well with energy consumption, calculated from observed food intake, and with measurements using doubly labelled water. It varied from 2.1 × *BMR* during the incubation stage to 2.7 × *BMR* during the chick-rearing stage. These values are much lower than the maximum energy expenditure reported for many other bird species during the reproductive cycle. During the chick-rearing stage, daily energy expenditure of leapfrogs was 6-7% higher than that of residents due to the additional costs involved in the transportation of food. Despite the fact that the reduced reproductive success of leapfrogs, as compared to that of residents, is mainly caused by the failure of the parents to provision their chicks with a sufficient amount of food, leapfrogs did not increase their parental effort to a considerable extent. This would fit the interpretation that long-living species like the Oystercatchers are reluctant to work very hard during one reproductive cycle.

Key words: Oystercatcher - *Haematopus ostralegus* - breeding - time budget - energy expenditure - double labelled water - energy consumption

Zoological Laboratory, University of Groningen, P.O. Box 14, 9750 AA Haren, The Netherlands. Present address: CNRS Chizé, 79360 Villiers en Bois, France.



INTRODUCTION

The theory of life-history evolution depends critically on the existence of a trade-off between current and future reproductive success (Stearns 1976). In semelparous species, parental effort is lethal; the parent dies immediately after the first reproductive attempt and hence there is no future

reproduction. In iteroparous species, parents are supposed to balance the benefits of an increased effort in the current attempt against the prospects for future attempts. Their maximum effort in the current attempt should enable them to stay alive and give them some chance to survive until the next season. The maximum and the realized level of parental effort by Oystercatchers *Haematopus ostralegus* breeding on the saltmarsh of Schiermonnikoog in the Dutch Wadden Sea are the subject of this paper.

Reproductive success of Oystercatchers differs with the type of territory occupied. The average number of fledglings produced per year is considerably larger in 'resident' than in 'leapfrog' territories (0.67 *versus* 0.19; Ens *et al.* 1995). The main distinction between resident and leapfrog territories is the distance between nesting and feeding area. These areas are adjacent to each other in resident territories but separated by 200-500 m in leapfrog territories. This distance becomes critically important during the chick-rearing stage. Since Oystercatchers are single prey loaders leapfrogs have to transport each prey to their chicks, while residents are followed by the chicks on the feeding grounds. Many leapfrog parents fail to provision their chicks with a sufficient amount of food and this was largely responsible for the difference in reproductive success between the two types of territory (Ens *et al.* 1992).

Resident territories are considered of higher quality than leapfrog territories because the owners require less parental effort to nourish the chicks. Increased parental effort can, potentially, compensate for breeding in a low quality territory, but this requires that time and energy is available. In this paper I compare the time and energy budgets of residents and leapfrogs throughout the breeding cycle. The main purpose is to quantify the level of parental effort and to determine whether time or energy constraints impose an upper limit to parental effort. Energy expenditure is used as a measure of parental effort.

Table 1. Exposure time (h) of the mudflats for residents and leapfrogs during subsequent stages of the breeding cycle.

	residents			leapfrogs		
stage	$\bar{x}$	*SD*	*n*	$\bar{x}$	*SD*	*n*
pre-laying	7.47	1.26	9	6.55	0.72	15
incubation	7.00	0.93	35	5.93	0.59	30
chick-rearing	6.93	0.65	21	5.66	0.77	61

METHODS

The study was conducted during the breeding seasons of 1985-1988 on the island of Schiermonnikoog (53°26'N, 6°13'E) in the Dutch part of the Wadden Sea. All Oystercatchers breeding in the 13-ha study area on the saltmarsh depended on the tidal mudflats for their food supply. Each bird was marked with a unique combination of colour rings. The data was collected between the end of April and the end of August.

The breeding season was divided into three stages: (1) the pre-laying stage ends when the clutch (normally 3-4 eggs) is completed and the birds start incubating; (2) the incubation stage covers the period between clutch completion and hatching of the last chick; (3) the chick-rearing stage ends when the last chick either fledges or dies. Since the breeding season of Oystercatchers is not very synchronized (clutch completion dates range from early May to the end of June), the actual transition date from one stage of the breeding cycle to the next differs between pairs. Therefore, we thoroughly searched the study area for new nests every four days from the end of April onwards and virtually all nests were discovered before the clutch was complete.

Time allocation and food consumption were determined for both members of a pair throughout an entire low water period (5-8 hours). During high water the level of activity is extremely low since the birds are resting or sleeping almost all of the time (Kersten unpubl.). The duration of low water periods varies with the two-week cycle of

spring and neap tides. Further, the exposure time of the feeding area is shorter for leapfrogs than for residents. Table 1 gives the average duration of low water periods for residents and leapfrogs at each stage of the breeding cycle.

During the low water period the birds were continuously observed with telescopes from observation towers. The data was stored in GECCO event recorders (an electronic device, designed and manufactured by Kees Rappoldt) with a time base of one second. Activity was classified into one of the following categories: foraging, resting, incubating, aggression, walking and flying. For practical reasons resting includes also time allocated to preening since the transition from preening to resting was often difficult to detect.

Conversion of time budget into energy budget

There are two approaches to convert time budgets into energy expenditure. One is to express measured or estimated costs of various activities as multiples of *BMR* (Basal Metabolic Rate: minimal, and highly reproducible, energy expenditure of an inactive, post-absorptive bird within the thermoneutral zone during the resting phase of its daily cycle) and add to these the costs for thermoregulation and, ideally, *HIF* (Heat Increment of Feeding: the energy that has to be invested during digestion in order to assimilate a larger amount of energy from the food). A potential problem with this approach is that it is rather obscure when Oystercatchers have their resting phase. Their lives are governed by the tides instead of by day and night and although they spend most of the high water period dozing, they are always alert and react immediately when something happens. They probably never sleep for an extended period of time and it seems unlikely that their energy expenditure in the field ever drops down to the *BMR* level.

An alternative approach is to start from *EM* (Existence Metabolism: energy expenditure at a specified temperature of captive birds with minimal activity which maintain their body weight) and add to these only the additional costs for various activities and that part of the *HIF* required to account for these additional costs. This method, initially advocated by Kendeigh (1974), has the advantage that it becomes less relevant whether the birds are sleeping or dozing, because both are included in *EM*. A further advantage is that the *EM*-part of *HIF* is already included in the measurement. I will follow both approaches and the conversion factors used will be quantified below.

(1) Basal Metabolic Rate. The *BMR* of Oystercatchers was measured by Speakman (1984) and Kersten & Piersma (1987) with comparable results. The average value was 2.91 Watt and a lower critical temperature of 10°C.

(2) Resting Metabolic Rate. *RMR* (Energy expenditure of an inactive bird during the active phase of the daily cycle) was assumed to be $1.8 \times$ *BMR*. Inactive birds both during high and low water were supposed to operate at this level of energy expenditure.

(3) Existence Metabolism. The relation between *EM* (kJ day^{-1}) and air temperature T_a in Oystercatchers is given by: $EM = 904 - 30.3T_a$ (Kersten & Piersma 1987). At air temperatures above 10°C, *EM* did not decrease any further and averaged 601 kJ day^{-1}. This value, which was recently confirmed by Goede (1993), is the average of measurements made during the summer when captive Oystercatchers are more active than during the remainder of the year. A reasonable estimate of the energy expenditure of birds with minimal activity can be derived from the lower part of the range of summer values, which is some 550 kJ day^{-1}.

(4) Thermoregulation. Additional energy expenditure to maintain a constant body temperature is required when air temperature drops under 10°C (see above). Daytime air temperatures hardly ever dropped under 10°C between May and August, when the data were collected, but minimum night temperatures sometimes did. Minimum night temperatures under 10°C averaged 6.3°C during the pre-laying stage, 9.0°C during the incubation stage and 9.3°C during the chick-rearing stage. Because these low temperatures lasted only a short time, just before sunrise, and the average temperature per 24 hours was

usually above 10°C, energy expenditure for thermoregulation is considered negligible.

(5) Walking. The energy expenditure during terrestrial locomotion increases linearly with velocity (Taylor *et al.* 1982). This linearity implies a constant energy expenditure per unit distance traveled, regardless of the velocity. We measured the oxygen consumption of Oystercatchers walking on a conveyer belt and derived an energetic cost of 4.85 J m^{-1} (Bruinzeel, Kersten & Piersma unpubl.). Consequently, the time spent walking has to be transformed into a distance traveled, which can subsequently be converted into additional energy expenditure. The average travel speed while walking is estimated at 0.30 m s^{-1}, i.e. two times as fast as birds foraging for *Nereis* (see below).

(6) Foraging for *Nereis* is not much more than walking. The modal travel speed is 0.15 m s^{-1} and about two prey items are captured per minute, which take only three seconds each to swallow (Ens *et al.* 1996). Occasionally, handling times are longer (up to 8 s), but this includes walking with the prey to a nearby pool to wash it. Foraging for *Macoma* is different; the modal travel speed is 0.05 m s^{-1} and birds spend up to 50% of the foraging time in opening and removing the shell. There are no measurements of the energy requirements for handling *Macoma*; it is almost certainly more demanding than walking at moderate velocities. On the other hand, *Macoma* is not a big prey and does not require a prolonged period of brutal force to open. A realistic and most convenient estimate of the energy requirements to handle *Macoma* is that it is twice the cost of walking. This makes the additional energy expenditure while foraging identical for all birds irrespective of the prey species. It should be mentioned that, although both prey are taken early in the season, most birds switch from *Macoma* to *Nereis* as the season progresses (Bunskoeke *et al.* 1996).

(7) Aggression. Energy expenditure during border disputes and the actual pursuit of intruders must be considerable since birds are moving around quickly and are obviously in a state of arousal. However these activities account for only a minor part of the time spent in aggression (roughly one-third). Most of the time the birds are merely bobbing, which is the Oystercatcher's way to assert itself, while moving slowly or not at all. An energy expenditure of 5 × *BMR* during physical involvement and *RMR* during the remainder of the time seems a reasonable assumption. This gives an average rate of 3 × *BMR* over all the aggression time (1.26 × *EM*).

(8) Incubation. Energy expenditure for incubation is in fact a special form of thermoregulation. The heart rate of incubating Oystercatchers was measured on Helgoland (8°00'E, 54°10'N). When a bird returned to its nest, heart rate was initially high, some 350 min^{-1}, since the bird had to warm the eggs. Heart rate declined rapidly to a steady state level of 152-168 min^{-1} after the bird had settled (Hüppop & Hagen 1990). The average steady state value (160 min^{-1}) is among the lowest heart rate ever recorded in Oystercatchers. Heart rate differs between individual birds; in four captive birds it varied between 176 min^{-1} and 205 min^{-1} under *BMR* circumstances (Kersten & Hüppop unpubl.). This indicates that the energy expenditure of an incubating bird under thermoneutral circumstances is close to *BMR*, and we used this value in our calculations.

(9) Flight. Attempts were made to measure flight costs directly using the doubly labelled water technique. Nineteen birds were displaced during the incubation stage and injected with doubly labelled water. They were released at distances varying between 8.8 km and 115 km from their nests. Eventually, all these birds returned; most of them after 1-2 days, but others took more than 4 days. Since they were very difficult to retrap, only nine birds could be recaptured before the isotopes had disappeared from the blood in measurable quantities. The time interval between release and recapture averaged 2.18 ± 1.00 days. This is very long compared to the actual flight time required to return, which is in the order of only two hours for the birds released at the most distant site. Consequently, the data had to be corrected to account for these non-flying hours. Unfortunately, the magnitude of these corrections was so large that a small error (3%) in the estimated energy expendi-

ture during the non-flying hours could either double the flight costs or reduce them to zero. Clearly, this makes these estimates unreliable and it was decided to derive flight costs from allometric relations.

There are several models to predict the energy expenditure during flight. Some of them are based on aerodynamic theory (Greenewalt 1975, Pennycuick 1975, 1989, Rayner 1979, 1990) while others are purely empirical, using body weight and one or more wing size variables as input (Hart & Berger 1972, Masman & Klaassen 1987, Videler 1995). The fit between model predictions and measured flight costs is generally poor for predictive purposes; differences up to 50% are not uncommon. Complications caused by different flight modes, the amount of soaring and gliding while on the wing, and the fact that energy expenditure changes with flight speed are probably responsible for these discrepancies. However, a recent evaluation revealed that for ground dwelling birds, characterized by a powerful flight mode, the empirically determined energy expenditure when flying at the maximum range speed is fairly accurately estimated by a simple allometric regression equation:

$$E_{flight} = 50.0W^{0.665} \ (n = 26 \text{ species}),$$

where E_{flight} is in Watts and W is body weight in kg (Videler 1995). Given an average body weight of 527 ± (*SD*) 27 g in ♂♂ and 537 ± (*SD*) 25 g in ♀♀, this gives an energy expenditure during flight of 32.7 and 33.1 Watt in male and female Oystercatchers respectively, which is equivalent to $11.3 \times BMR$.

(10) Heat increment of feeding. A reliable estimate states that 20% of the total amount of energy assimilated is expended in *HIF*. This value was determined on captive Turnstones *Arenaria interpres* eating commercial food pellets with a composition and digestibility almost identical to the food of our Oystercatchers (Klaassen *et al.* 1990). This value is slightly higher than the 15% *HIF* measured in chicks of the Adélie Penguin *Pygoscelis adeliae* (Janes & Chappell 1995). As mentioned above, *HIF* is to a large extent already included in *EM*. We have to account only for that part of the *HIF* which is due to the additional energy expenditure on top of *EM*.

Food intake

Food consumption was determined by recording type and size of each prey item consumed. The vast majority of prey taken were either Ragworms *Nereis diversicolor* or small bivalves *Macoma balthica*. Larger bivalves were taken occasionally. These include: Cockle *Cerastoderma edule*, Sandgaper *Mya arenaria* and Mussel *Mytilus edulis*. The shells of bivalves were always opened and only the flesh was ingested. The size of flesh particles was scored in arbitrary size classes from 1 to 9, where size class 4 referred to an item roughly the size of the colour ring. The length of *Nereis* was scored in 2-cm classes with reference to the bill length of the bird (on average 7 cm in ♂♂ and 8 cm in ♀♀, Hulscher 1985). Prey size was translated into biomass (ash-free dry weight) using the conversion factors given by Kersten and Brenninkmeijer (1995). An independent check on the reliability of the estimated prey weight was performed by Kersten and Visser (1996) using the weight increase of the adult during a feeding period in between two incubation spells on a nest balance.

The energy content of macrobenthic prey has been studied extensively by Zwarts & Wanink (1993), who demonstrated considerable variation with latitude (energy content generally increased with latitude) but little variation between prey species in one locality. The tellinid bivalve *Macoma balthica* and the ragworm *Nereis diversicolor* were the dominant prey species taken by our study population. In the Dutch Waddensea, the energy content of these prey species was similar and we used the average value of 22.1 kJ g^{-1} AFDW as the energy equivalent to convert biomass consumed into energy. Assimilation efficiency was taken as 85% (Kersten & Visser 1996).

Doubly labelled water

Upon capture, a small blood sample was collected from one leg to determine the background

Table 2. Time budget of resident Oystercatchers at various stages of the breeding cycle. Given is the average percentage of time per low water period allocated to each behaviour. Differences between ♂ and ♀ were tested with Mann-Whitney *U*-tests. The behavioral category 'other' includes time devoted to copulations and nest building during the pre-laying stage and time spent brooding small chicks during the chick-rearing stage; as well as the time that we could not keep trace of the bird. Number of cases for ♂♂ and ♀♀, respectively: prey-laying: 4 and 5, incubation: 13 and 13, and chick-rearing: 11 and 10.

	♂♂		♀♀		*U*	*p*
	$\bar{x}$	*SD*	$\bar{x}$	*SD*		
pre-laying						
foraging	48.9	23.8	47.4	8.4	9	0.904
inactive	34.5	17.1	42.3	10.5	7	0.556
aggression	11.2	6.5	5.4	1.9	5	0.286
walking	2.4	1.5	2.8	1.3	9	0.904
flying	1.6	0.5	1.0	0.4	3	0.112
other	1.4	2.2	1.1	0.9		
incubation						
foraging	23.2	9.1	27.3	7.1	53	0.101
inactive	19.4	11.4	25.8	14.9	82	0.898
incubation	44.0	15.3	34.4	20.9	82	0.898
aggression	7.2	3.7	4.0	2.3	40	0.029
walking	4.0	1.3	5.8	2.6	56	0.137
flying	1.4	0.8	1.0	0.6	65	0.316
chick-rearing						
foraging	34.6	15.3	30.9	17.8	52	0.754
inactive	38.3	12.3	34.9	14.6	47	0.547
aggression	13.0	7.9	18.4	15.0	45	0.460
walking	8.2	3.2	9.2	1.6	36	0.172
flying	3.0	2.4	2.8	3.1	46	0.526
other	1.4	2.2	1.1	0.9		

levels of the stable isotopes ^{2}H and ^{18}O. Subsequently, the birds were injected intraperitoneally with a mixture of $H_2{}^{18}O$ (90.23 atom%) and $^{2}H_2O$ (99.84 atom%). The amount injected varied with the expected duration of the experiment. After an equilibration period of at least three hours, the initial blood sample was taken from the other leg. The bird was weighed to the nearest gram before release. A final blood sample was collected upon recapture. The blood samples were analysed for isotopic enrichment at the Center of Isotope Research, University of Groningen, by means of mass spectrometry. The water content of the bird was estimated at 68% of its body weight. Daily energy expenditure was calculated from the isotope turnover rates using the two compartments model (Heyman & Roberts 1990), assuming an average dilution space ratio of 1.04, the fraction of water lost through evaporation as 0.1 and an energy equivalent of 26 kJ/l CO_2.

RESULTS

Time budgets of residents and leapfrogs

The time budgets during low water were very similar for ♂♂ and ♀♀ throughout the breeding season. This was true for both residents (Table 2) and leapfrogs (Table 3). Small, but statistically significant differences occurred during the incu-

Table 3. Time budget of leapfrog Oystercatchers at various stages of the breeding cycle. Given is the average percentage of time per low water period allocated to each behaviour. Differences between ♂ and ♀ were tested with Mann-Whitney *U*-tests. The behavioral category 'other' includes time devoted to copulations and nest building during the pre-laying period and time spent brooding small chicks during the chick-rearing period; as well as the time that we could not keep trace of the bird. Number of cases for ♂♂ and ♀♀, respectively: prey-laying: 7 and 7, incubation: 14 and 16, chick-rearing: 31 and 31.

	♂♂		♀♀		*U*	*p*
	$\bar{x}$	*SD*	$\bar{x}$	*SD*		
pre-laying						
foraging	39.4	18.6	44.6	19.6	23	0.866
inactive	48.8	18.7	45.2	18.9	23	0.866
aggression	6.1	2.7	5.7	4.0	20	0.396
walking	1.9	1.3	1.8	1.0	22	0.536
flying	2.2	0.9	1.4	0.8	13	0.094
other	1.6	1.4	1.3	1.2		
incubation						
foraging	20.3	8.0	22.3	10.4	101	0.645
inactive	26.0	14.9	22.5	16.8	93	0.429
incubation	40.2	17.9	46.9	24.7	88	0.318
aggression	5.2	3.7	1.4	1.8	40	0.003
walking	4.8	1.6	4.6	3.1	95	0.478
flying	3.5	1.5	2.3	0.9	57	0.022
chick-rearing						
foraging	35.9	18.0	37.2	16.8	473	0.918
inactive	43.4	20.1	42.3	17.5	471	0.900
aggression	6.5	5.5	4.8	6.2	355	0.077
walking	4.6	3.8	3.3	3.3	387	0.188
flying	7.6	3.9	8.6	4.3	435	0.522
other	2.0	5.3	3.8	9.8		

bation stage, when ♂♂ spent slightly more time in aggressive encounters then did ♀♀ (residents: $p = 0.029$; leapfrogs: $p = 0.003$, Mann-Whitney *U*-tests).

Regarding the marginal differences between the sexes we lumped the data of ♂♂ and ♀♀ to compare the time budget of pairs occupying resident or leapfrog territories (Table 4). The time allocated to the three main behavioural categories, foraging, inactivity and incubating, did not differ significantly between the two types of territory. Residents spent more time in aggression during the incubation ($p < 0.05$) and chick-rearing ($p < 0.001$) stages and walked more during the chick-rearing stage ($p < 0.001$), whereas leapfrogs spent more time in flight during both the incubation and chick-rearing stage ($p < 0.001$ in both cases, Mann-Whitney *U*-test). This conforms to the general impression that the type of territory occupied has little effect on the allocation of time to various activities. Throughout the breeding cycle foraging and inactivity dominate the low water period, while incubating adds to these two during the incubation period. The main differences occur during the chick-rearing period and involve the level of aggression (higher in residents) and the mode of locomotion (flying in leapfrogs, walking in residents).

The time budget throughout the breeding cycle

In both residents and leapfrogs, time budgets

Table 4. Time budget of resident and leapfrog Oystercatchers (sexes combined) at various stages of the breeding cycle. Given is the average percentage of time per low water period allocated to each behaviour. Differences between residents and leapfrogs were tested with Mann-Whitney *U*-tests. Number of cases for ♂♂ and ♀♀, respectively: prey-laying: 9 and 14, incubation: 35 and 30, chick-rearing: 21 and 62.

	residents		leapfrogs		*U*	*p*
	$\bar{x}$	*SD*	$\bar{x}$	*SD*		
pre-laying						
foraging	48.1	15.7	41.9	18.6	54	0.571
inactive	38.9	13.5	47.0	18.1	56	0.667
aggression	8.0	5.2	5.9	3.3	48	0.345
walking	2.6	1.3	1.8	1.1	40	0.148
flying	1.2	0.6	1.8	0.9	42	0.186
incubation						
foraging	23.6	9.8	21.4	9.3	435	0.238
inactive	20.8	14.3	24.1	15.8	448	0.317
incubation	44.3	15.3	43.8	20.9	498	0.719
aggression	5.6	3.6	3.2	3.3	295	0.026
walking	4.7	2.4	4.7	2.5	508	0.826
flying	1.0	0.8	2.8	1.4	115	0.000
chick-rearing						
foraging	32.8	16.3	36.7	17.2	568	0.384
inactive	36.7	13.2	42.9	18.5	542	0.254
aggression	15.6	11.8	5.5	5.9	208	0.000
walking	8.7	2.5	3.9	3.6	149	0.000
flying	2.9	2.6	8.2	4.1	170	0.000

change dramatically with the stage in the breeding cycle (Fig. 1). When the clutch is completed, the necessity to incubate the eggs competes for time with other activities. Each individual allocated on average 44% of the time to incubation. As a result, the proportion of time spent in all other activities is reduced by almost 50% with one exception. The time spent walking doubled, which is mainly due to the careful way in which birds approach their nest.

As soon as the eggs have hatched, the birds are committed to care for their chicks. This had a pronounced effect on the time budget which differed between the two types of territory. Residents spent more than 15% of the time in aggression, mainly border disputes with their neighbours. The proportion of time spent inactive increased to pre-laying levels, but the foraging time of parents with chicks was significantly less than the time spent foraging during the pre-laying stage ($U = 41$, $z = 2.42$, $p < 0.01$). Leapfrog parents increased their flight time from 2.8% to 8.2% ($U = 51$, $p < 0.001$), while the time spent inactive or foraging increased (inactive: $U = 382$, $p < 0.001$; foraging: $U = 413$, $p < 0.001$), reaching pre-laying levels. The increased flight time reflects the fact that leapfrogs had to transport the food for the chicks by air: from distant feeding areas, over the resident territories to their nesting territory on the marsh.

Estimated energy expenditure

The consequences of these changes in time allocation for the energy budget are tabulated in Table 5 (*BMR*-approach) and Table 6 (*EM*-approach). It should be realized that the energetic

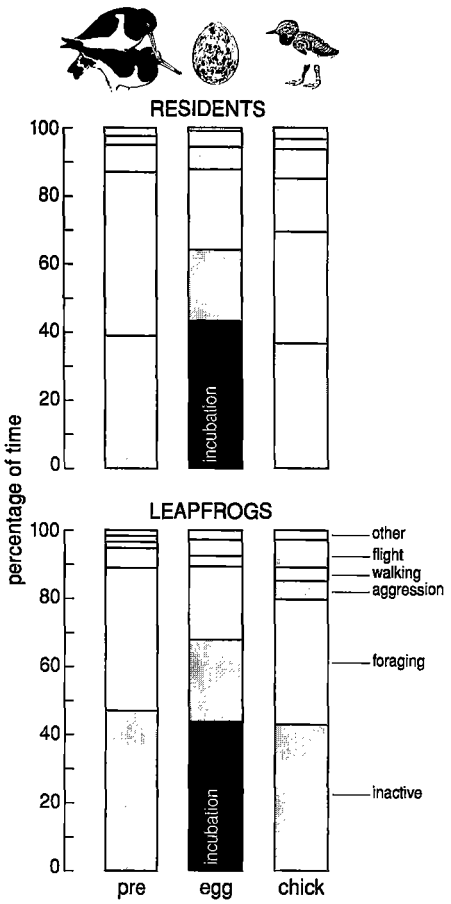


Fig. 1. Time budget (% of time during low water period) of resident and leapfrog Oystercatchers during the pre-laying, incubation and chick-rearing stage.

terms associated with the various activities have an entirely different meaning in the two tables. In the *BMR*-approach, the values represent total energy expenditure while the bird is performing that particular activity. In the *EM*-approach, the values represent the additional amount of energy expended by performing this activity instead of remaining inactive. For instance, the total amount of energy expended by male residents while foraging during the pre-laying stage is 157 kJ day^{-1}, which looms large in its daily energy budget (Table 5). However, this is entirely due to the fact that the bird forages for about 25% of the time; the additional energy expended because of foraging is estimated at only 19 kJ day^{-1} (Table 6), indicating that foraging is not an energy consuming activity.

At all stages of the breeding cycle, most energy is expended while the birds are inactive. Only two activities have such a pronounced effect on the energy budget that they alone can account for almost all changes in energy expenditure during the breeding cycle. Incubating eggs leads to a considerable reduction, while flying induces an increase of estimated daily energy expenditure. The impact of all other activities appears rather small.

In both approaches, energy expenditure is lowest during the incubation stage and highest during the chick-rearing stage. There is generally a good agreement between the estimated energy expenditure from the two approaches. The main difference occurs during the incubation stage when the estimate based on *EM* is on average 10% lower than that based on *BMR*.

Food consumption per low water period

Calculating total food consumption over the entire low water period from the number and size of prey recorded was sometimes hampered by the habit of the birds to collect some food outside of their territories. This occurred in residents mainly during the pre-laying and incubation stage. Once the chicks were hatched, foraging outside the territory decreased suddenly from about 40% to 5% of the time spent foraging (U = 606, p = 0.009, Fig. 2). In leapfrogs, foraging outside of the territory peaked during the incubation stage when almost half of all foraging was done outside the territory (Fig. 2). During the pre-laying and chick-rearing stage, the percentage of foraging time outside the territory was significantly less and averaged about 30% (pre-laying stage: U = 156.5, p = 0.011; chick-rearing stage: U = 110, p = 0.034). The areas visited were located 1-2 km downshore where food intake could not be quantified. However, indirect measurements of food consumption, based on the weight change of birds incubating on a nest balance demonstrated that the food

Table 5. Estimated energy expenditure (kJ day^{-1}) of adult Oystercatchers at various stages of the breeding cycle derived from the time budgets following the *BMR*-approach (see methods). The values represent the amount of energy expended while performing each activity.

	pre-laying		incubation		chick-rearing	
	♂	♀	♂	♀	♂	♀
residents						
foraging	157	152	70	83	103	93
inactive	269	291	155	156	292	283
aggression	53	25	27	21	57	80
walking	9	10	14	19	27	31
flying	28	18	20	17	49	46
incubation	0	0	112	110	0	0
other	4	4	7	0	9	11
HIF	104	100	81	81	107	109
total	624	600	486	487	644	653
leapfrogs						
foraging	110	126	52	57	88	90
inactive	328	318	170	170	333	331
aggression	25	24	19	5	23	17
walking	6	6	14	12	13	9
flying	34	22	49	33	101	116
incubation	0	0	108	116	0	0
other	4	4	0	0	5	9
HIF	102	100	82	79	112	115
total	609	600	494	472	675	687

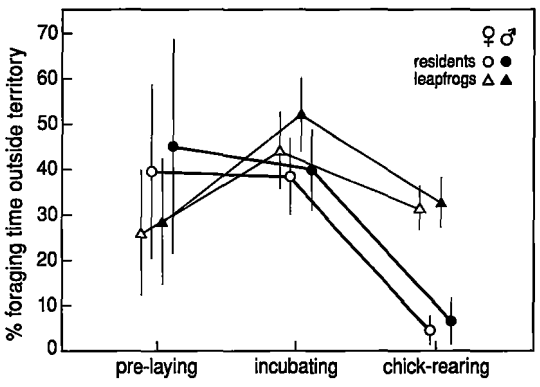


Fig. 2. The proportion of foraging time spent outside the territory by residents and leapfrogs at various stages of the breeding cycle. Vertical bars denote one standard error of the mean. ♂♂ and ♀♀ spent equal proportions of foraging time outside the territory (Mann-Whitney *U*-tests, $p > 0.05$ in each case). During the pre-laying stage, residents spent more time foraging outside the territory than leapfrogs, but this difference was not significant ($U = 94.5$, $p = 0.479$). During the chick-rearing stage, residents spent significantly less time outside the territory than leapfrogs ($U = 131.5$, $p < 0.001$).

intake rate downshore was similar to the food intake rate while foraging in the territory (Kersten & Visser 1996). Since the time that birds were absent from their territories was always recorded, we estimated the amount of food collected outside the territory by each bird from the product of time outside and the average intake rate of that particular individual within its territory.

At all stages of the breeding cycle and both in residents and leapfrogs, ♀♀ consumed on aver-

Table 6. Estimated energy expenditure (kJ day^{-1}) of adult Oystercatchers at various stages of the breeding cycle derived from the time budgets following the *EM* (Existence Metabolism) approach (see methods). The values represent the additional amount of energy expended while performing each activity on top of the amount that should have been expended when the bird showed minimal activity (*EM*). In the case of *HIF* (Heat Increment of Feeding), the values represent 20% of the difference between energy expenditure in captivity and in the field.

	pre-laying		incubation		chick-rearing	
	♂	♀	♂	♀	♂	♀
residents						
EM	550	550	550	550	550	550
foraging	19	19	9	10	13	11
aggression	15	8	8	6	16	23
walking	2	2	13	4	6	7
flying	22	14	16	13	38	36
incubation	0	0	–132	–130	0	0
HIF adjustment	15	10	–24	–24	18	19
total	623	603	430	429	641	646
leapfrogs						
EM	550	550	550	550	550	550
foraging	14	15	6	7	11	11
aggression	7	7	6	2	7	5
walking	1	1	3	3	3	2
flying	27	17	38	25	80	92
incubation	0	0	–127	–136	0	0
HIF adjustment	12	10	–19	–25	25	27
total	611	600	457	426	676	687

age more food per low water period than did ♂♂, but the difference was never significant (Table 7). The largest difference occurred during the pre-laying stage, when ♀♀ are faced with the additional burden to produce the eggs. The difference amounted to 6.28 g AFDW in residents and 4.90 g AFDW in leapfrogs. Due to the relatively small sample sizes together with the large scatter in the data, related to the fact that Oystercatchers do not have to match food intake with energy requirements on a time scale of only one low water period (Kersten & Visser 1996), this marked difference is not statistically significant. Increasing sample size by lumping the data of residents and leapfrogs increased the performance of the *t*-test slightly, but the result was still not statistically significant (♂♂: 19.23 ± 9.10 g AFDW, $n = 13$; ♀♀: 24.39 ± 9.16 g AFDW, $n = 14$; $t = 1.468$, $df = 25$, $p = 0.16$). An alternative way to tackle this problem is to look at the reduction of food intake between the pre-laying and incubation stage of the breeding cycle. Both ♂♂ and ♀♀ reduce their food consumption per low water period when they enter the incubation stage, but the decline is much larger in ♀♀ than in ♂♂. Among residents, the reduction is 6.2 g AFDW in ♀♀ compared to 2.4 g AFDW in ♂♂. Among leapfrogs, the reduction is 11.3 g AFDW in ♀♀ compared to 6.8 g AFDW in ♂♂. As the additional costs for egg production are likely to be the same in residents and leapfrogs, we lumped the data to test whether the reduction was larger in ♀♀ (8.56 ± (*SE*) 1.50 g, $n = 56$) than in ♂♂ (4.12 ± (*SE*) 1.55 g, $n = 48$). This difference between the sexes of 4.44 g AFDW was significant ($p < 0.01$, *t*-test).

Table 7. Food consumption (g AFDW) per low water period of adult Oystercatchers occupying resident and leapfrog territories during subsequent stages of the breeding cycle. Differences between ♂♂ and ♀♀ were tested with Student's *t*-test.

	♂♂			♀♀			
	$\bar{x}$	*SD*	*n*	$\bar{x}$	*SD*	*n*	*p*
residents							
pre-laying	16.0	7.8	4	22.2	5.1	5	0.19
incubation	13.6	5.2	20	16.0	6.8	25	0.42
chick-rearing	16.6	3.8	11	17.1	5.2	8	0.81
leapfrogs							
pre-laying	20.7	9.7	9	25.6	10.9	9	0.33
incubation	13.9	5.6	14	14.3	5.7	17	0.73
chick-rearing	18.1	9.3	28	18.1	8.2	28	0.99

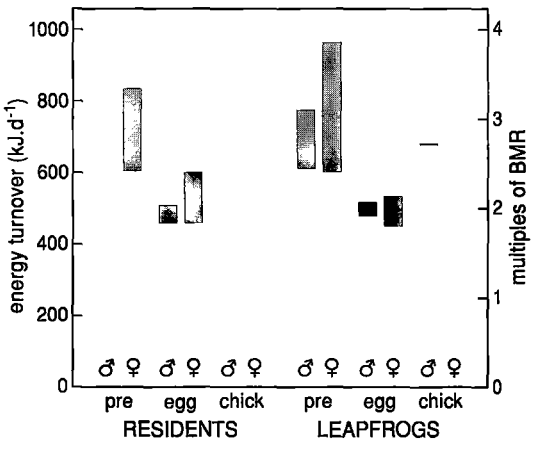


Fig. 3. Daily energy turnover in adult Oystercatchers during various stages of the breeding cycle. The light-shaded bars represent the estimated energy expenditure based on the time budgets (average values of Tables 5 and 6). The dark-shaded bars indicate that more energy was assimilated.

Daily energy intake and expenditure

Given that there are two low water periods per 24 hours, and for the local diet an energy equivalent of 22.1 kJ g^{-1} AFDW ingested (see methods and Zwarts & Wanink 1993) with an energy assimilation efficiency of 85%; the amount of energy assimilated per day was calculated and compared with estimated energy expenditure based on the time budgets (Fig. 3). Although there was a general agreement between income and expenditure, some remarkable differences were revealed as well.

During the incubation stage, energy income was systematically higher than estimated expenditure. The difference, which averaged 83 kJ day^{-1}, might be due to an error in one of the estimates or may indicate that Oystercatchers deposit energy reserves during the incubation stage. The available evidence does not support the latter possibility. Digesta-free body weight of birds incubating on a balance tended to remain stable throughout the incubation period (Fig. 4). The most likely explanation for the discrepancy is that the energy expenditure of incubating birds is underestimated. Although Hüppop & Hagen (1990) reported a very slow heart rate during prolonged incubation, the average rate of energy expenditure while incubating is probably well above *BMR*. This is partly due to the fact that Oystercatchers rarely remained on the eggs for a long spell. Usually, they left the nest at least once per hour. Since the eggs cool down during their absence, the birds have to warm them upon return and this may require a substantial amount of energy. Despite this probable underestimation, the incubation stage remains the period with the lowest energy expenditure during the breeding cycle.

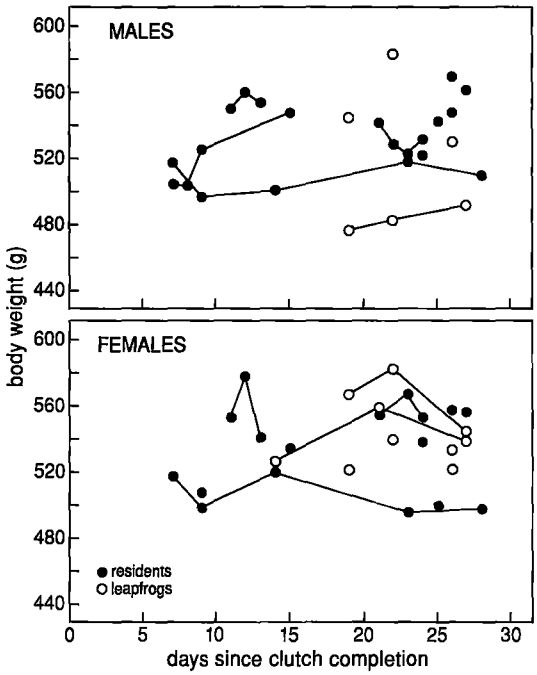


Fig. 4. Digesta-free body weight of Oystercatchers at the end of a high water period, when there is no food left in the digestive tract. Data refer to birds incubating on a nest balance and lines connect measurements of the same individual.

The highest energy intake was realized by ♀♀, residents as well as leapfrogs, during the pre-laying stage. This was not accompanied by an unusually high energy expenditure. As mentioned above, this positive energy balance almost certainly reflects the energy required to form the eggs. There is one discrepancy in Fig. 3 for which there is no obvious explanation: male leapfrogs collect substantially more energy during the pre-laying stage than they expend (777 *versus* 610 kJ day^{-1}). Since the time budget of male leapfrogs is similar at this stage to that of male residents, it seems unlikely that energy expenditure is underestimated. Two possibilities remain. One is that energy income is overestimated due to random bias in our sampling. The other possibility is that male leapfrogs do indeed have a positive energy budget during the pre-laying stage and increase their body weight. Although it was not possible to measure body weight before clutch completion, there is some indirect support for the latter possibility. Male leapfrogs hardly leave the nesting territory on the marsh once there are two eggs in the clutch, but there is still more to come. Two measurements of energy income during this period averaged 261 kJ day^{-1} for ♂♂ compared to 616 kJ day^{-1} for ♀♀. Since the estimated energy expenditure of the ♂ is 610 kJ day^{-1}, this entails an energy deficit of 349 kJ day^{-1}, which accumulates over a three day period until the fourth egg is laid to 1047 kJ. Given this large energy deficit, which is equivalent to 26 g fat, it would not be surprising if male leapfrogs prepare themselves for this situation and deposit an energy reserve in

Table 8. Energy expenditure of individual Oystercatchers measured with doubly labelled water. The first leapfrog ♂ measured during the chick-rearing stage reduced its flight time after injection by some 50%. Abrevations: inc = incubation, chk = chick-rearing, res = resident, lpf = leapfrog. The birds mentioned on line 1 and 3 and on line 2 were displaced 26 and 8.8 km, respectively.

date	stage	status	sex	weight g	interval min	energy kJ day^{-1}	expenditure × *BMR*
26-5-1986	inc	res	♀	516	1700	995	3.95
29-5-1987	inc	res	♀	574	2540	600	2.38
3-6-1987	inc	lpf	♂	534	5550	776	2.80
18-6-1987	inc	res	♂	491	2865	400	1.59
24-6-1986	chk	lpf	♂	480	1335	669	2.65
9-7-1986	chk	res	♂	534	1350	743	2.95
31-7-1986	chk	lpf	♂	463	1340	712	2.83

Table 9. Most realistic estimates of daily energy expenditure of adult Oystercatchers throughout the breeding season, expressed in kilojoules and as multiples of *BMR* (2.91 Watt or 251 kJ day^{-1} according to Kersten & Piersma 1987). These values are based on the time-energy budgets during the pre-laying and chick-rearing stage and on measurements of food intake during the incubation stage since energy requirements for incubating the eggs was probably underestimated see text).

	pre-laying		incubation		chick-rearing	
	kJ	× *BMR*	kJ	× *BMR*	kJ	× *BMR*
residents						
♂♂	624	2.49	511	2.03	643	2.56
♀♀	602	2.40	603	2.40	650	2.59
leapfrogs						
♂♂	610	2.43	522	2.08	676	2.69
♀♀	600	2.39	536	2.13	687	2.74

advance. Male residents do not face this problem as their feeding territory is adjacent to the nesting area and they are able to keep an eye on the eggs while foraging.

Due to difficulties with recapturing the birds, only a few direct measurements of energy expenditure using the doubly labelled water technique were successfully completed. These are listed in Table 8. Some of the measurements during the incubation stage include a return flight trip after displacement (see methods). Further, the first leapfrog ♂ measured during the chick-rearing stage reduced its flight time from about 1600 s per low water period before the experiment to 795 s during the first low water period after release. Nonetheless, the measured rates of energy expenditure are in the same range as the estimated energy expenditure based on the time budgets and food consumption (Table 9).

DISCUSSION

Time budgets and the existence of surplus time

The activity pattern and energy expenditure of ♂♂ and ♀♀ hardly differed throughout the breeding cycle. Both sexes contributed equally to the activities required to raise their offspring. Within a pair, there may be some division of labour, but the decision who is going to do what is not governed by gender. Likewise, the time budgets of Oystercatchers occupying resident and leapfrog territories were remarkably similar. The main difference occurred during the chick-rearing stage when leapfrogs increased their flight-time in order to transport food to their chicks.

The most striking feature in the time budgets is the prevalence of a considerable proportion of time which is spent inactive. Even during the incubation stage when the necessity to incubate the eggs competes heavily for time with other activities, both residents and leapfrogs did remain inactive for 20-24% of the low water period. Although time allocated to foraging is also significantly reduced during this stage, the persistence of time spent idle indicates that foraging is, on average, not constrained by the time allocated to incubation. This suggests that time spent inactive is in fact 'surplus time' which can be used for more productive activities when the circumstances require it.

As there is a lot of natural variation in the proportion of time spent incubating during a low water period, I used this variation to investigate whether time spent inactive is indeed relocated to foraging when time becomes a precious commodity. Figure 5 shows that time spent foraging remained constant at 29.5 ± 7.7% (*SD*) in residents and 25.5 ± 8.4% (*SD*) in leapfrogs as long as the proportion of time spent incubating did not ex-

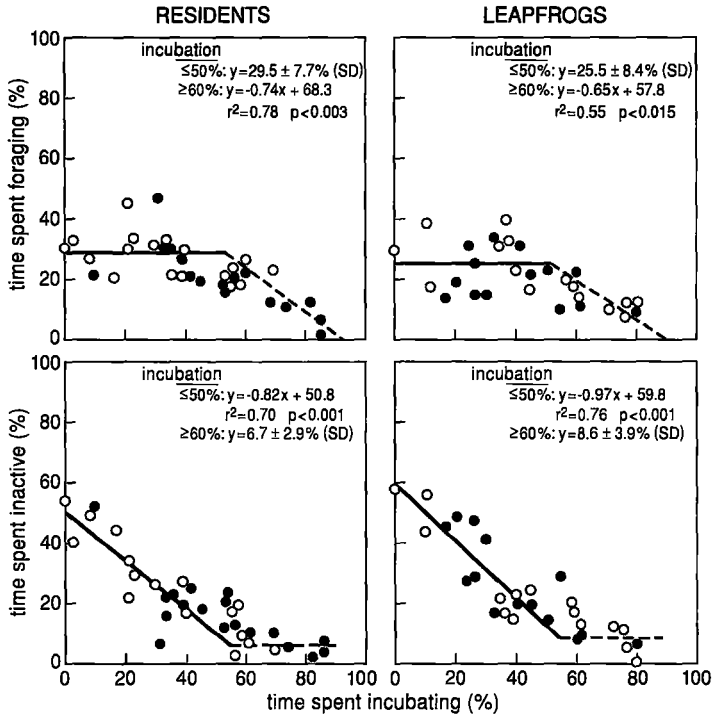


Fig. 5. Percentage of time allocated foraging and inactivity by residents and leapfrogs during the incubation stage in relation to the time devoted to incubating. The shaded areas represent the possible combinations.

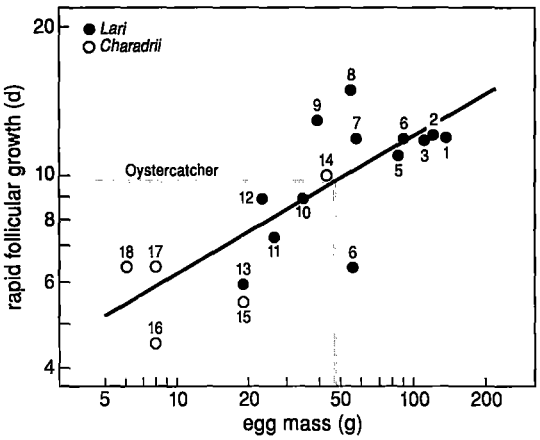
ceed 50% of the low water period. Within this range of incubation times, the slopes of the linear regression equations between foraging time and time spent inactive did not differ significantly from zero (residents: $R^2 = 0.03$, $n = 19$, $p = 0.57$: leapfrogs: $R^2 = 0.00$, $n = 18$, $p = 0.98$). When the proportion of time allocated to incubation increases further, foraging time has to decline eventually. The data suggests that foraging time becomes constrained only after more than 60% of the low water time is allocated to incubation, but even then foraging time decreases by only about 0.7% for every 1% increase of the time allocated to incubation. At the same time, the proportion of time spent inactive decreased sharply from 50-60% down to less than 10% of the low water period when the time allocated to incubation increased from 0% to 50% (residents: slope = –0.82 ± 0.13 (*SEE*), $R^2 = 0.70$, $n = 18$, $p < 0.001$; leapfrogs: slope = –0.97 ± 0.13 (*SEE*), $R^2 = 0.76$, $n = 18$, $p < 0.001$). When time allocated to incubation increased even further, inactivity did not disappear completely but remained more or less stable at 6.7% in residents and 8.6% in leapfrogs. These low values probably represent an obligatory inactivity time which cannot be relocated to other activities. Some of this time is required for preening while the remainder is 'lost' during the transition from one behaviour to the other; for instance when birds waited a short while after an aggressive interaction before they decided to resume foraging or to return to the nest to incubate the eggs.

The highest level of inactivity occurs during the pre-laying stage when birds were inactive for on average more then 40% of the low water period (Tables 2 & 3). This coincides for the ♀♀ with the highest food consumption of the season (Fig. 3). Female food consumption averaged 898 kJ day^{-1} during this stage, which is 84% of the maximum amount that Oystercatchers are able to process during a 24 hour day (Kersten & Visser 1996). Considering these figures it is possible that digestive pauses were responsible for some of the

time spent inactive. Whether or not a digestive bottleneck was involved, these data underline once again that at this time of the year Oystercatchers can indeed collect the maximum amount of food that they are able to process in a remarkably short time. Since food consumption was much smaller during the later stages of the breeding cycle, it is unlikely that digestive pauses were responsible for the time spent inactive during these stages.

Female food consumption during egg formation

Food consumption of ♀♀ peaked during the pre-laying stage and was 235-362 kJ.day–1 higher than their energy expenditure. The surplus is thought to be related to the additional requirements for egg production. The average fresh weight of Oystercatcher eggs is 46 g (Jager & Kersten upubl.). The shell accounts for 9.0% of fresh weight, while most of the contents is water (68.7%). Dry lipids contribute 9.0% and dry proteins 13.3% of the fresh weight. Given an energy equivalent of 39.5 kJ g^{-1} fat and 23.6 kJ g^{-1} dry protein (Brody 1945), the total amount of energy deposited in one egg becomes ($0.09 \times 46 \times 39.5 + 0.133 \times 46 \times 23.6$ =) 308 kJ. Assuming a 77% efficiency of egg production, comparable to that of the domestic fowl (Brody 1945), the total amount of energy involved in the production of a typical four-egg clutch is ($4 \times 308 \times (100/77)$ =) 1600 kJ. The observed surplus food consumption would enable ♀♀ to collect all the energy for the entire clutch in 5-7 days. This is much faster than necessary. An allometric regression between egg weight and the duration of rapid follicular growth among charadriform birds (Fig. 6) estimates that a 46 g egg requires just under ten days to be produced. Oystercatchers are almost certainly capable of achieving a better performance, since the earliest replacement clutches were initiated eight days after the original clutch disappeared (Jager & Kersten unpubl.). Eggs within a clutch are produced at approximately 36-hours intervals, so the total duration of clutch production is about 12.5 days. This would require a surplus food consumption of 128 kJ day^{-1}, which is only 35-54% of the observed surplus food intake. It remains obscure why the observed food intake is much higher than expected during the pre-laying stage. A weak point in our estimate of female food consumption is that we have assumed that food consumption at night equals that during the day. We have no data on night-time food intake during this stage of the breeding cycle as we do have during the incubation stage. Since birds were able to match daytime performance later in the season, it is unlikely that the intake rate at night is reduced. But it is possible that ♀♀ spent less time feeding at night. However, night-time observations on Texel at the start of the breeding season (April and May) revealed that the density of birds feeding on the mudflats was comparable between day and night



1 *Larus marinus*
2 *Larus hyperboreus*
3 *Larus glaucescens*
4 *Larus argentatus*
5 *Larus occidentalis*
6 *Larus canus*
7 *Larus delawarensis*
8 *Risa tridactyla*
9 *Larus novaehollandiae*
10 *Sterna fuscata*
11 *Anous minutus*
12 *Gygis alba*
13 *Sterna paradisea*
14 *Limosa lapponica*
15 *Arenearia interpres*
16 *Phalaropus falicarius*
17 *Calidris mauri*
18 *Phalaropus lobatus*

Fig. 6. The relation between egg mass and the duration of egg formation in Laridae and Charadrii. The data were retrieved from Astheimer & Grau (1990) and Roudybush *et al.* (1979). The allometric regression equation is given by the formula: $Y = 3.24716X^{0.28642}$, $R^2 = 0.60$, $n = 20$.

(B.J. Ens pers. comm.). Another possibility is that ♀♀ too lay down some energy reserves to draw upon immediately after clutch completion, as do ♂♂ prior to laying, but there is no data to confirm this.

Energy expenditure

Throughout the breeding cycle energy expenditure is rather low in both residents and leapfrogs. The most realistic estimates of energy expenditure are listed in Table 9. Expressed as multiples of *BMR*, energy expenditure was only 2.2 × *BMR* during the incubation stage and barely reached the 2.7 × *BMR* mark during the chick-rearing stage. Compared to other bird species this last figure is very low, given that the energy expenditure of parents feeding offspring is usually well above 3 × *BMR* (Bryant & Tatner 1991). Apparently, Oystercatchers operate at a much lower level which is remarkable with respect to the leapfrogs, since chick starvation is considered the main factor responsible for their low reproductive success (Ens *et al.* 1992). During the chick-rearing stage leapfrog energy expenditure averaged 682 kJ day^{-1}, which is 5% higher than that of residents. This marginal increase of parental effort was in no way sufficient to compensate for the lower quality of their territories. It seems unlikely that an energetic constraint precluded them from a higher level of parental effort, since the maximum sustained working level is estimated at 1067 kJ day^{-1} (Kersten & Visser 1996).

Despite the fact that neither time nor energy seemed to be in short supply, leapfrogs failed to increase parental effort any further in order to compensate for the negative effect of territory quality on their reproductive success. The theory of life-history evolution depends critically on the existence of a trade-off between the allocation of resources to current versus future reproduction (Stearns 1976). Such a trade-off may be responsible for the unwillingness of leapfrogs to increase their parental effort, but this raises some questions concerning the mechanism involved. A reduction of future reproductive success may be caused by increased mortality or reduced fecundity during subsequent breeding seasons. It is unlikely that reduced fecundity prevents leapfrogs from increasing their parental effort. Reproductive success of leapfrogs is at best one chick raised to fledging per season (Ens *et al.* 1992). Established pairs rarely forego a breeding attempt in any one year (pers. obs.), so the trade-off is between raising a chick either this year or next year. Since a chick raised this year contributes more to an individual's inclusive fitness than a possible one reared in the future, such a trade-off would, in the absence of any survival cost, favour increase of effort in the present attempt. This suggests that a potential fitness cost associated with increased parental effort is more likely related to a higher risk of mortality. Increased mortality of parents raising experimentally increased brood sizes was reported in some studies (Askenmo 1979, Reid 1987, Dijkstra *et al.* 1990, Deerenberg *et al.* 1995,

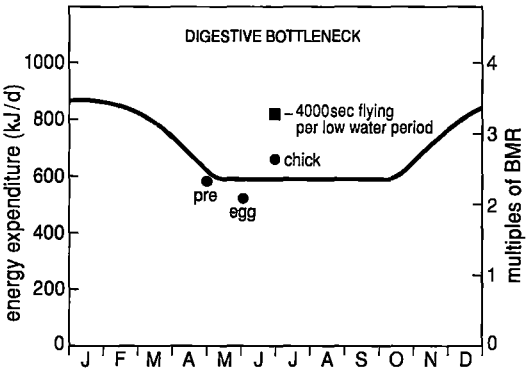


Fig. 7. Estimated energy expenditure of free-living Oystercatchers during the pre-laying, incubation and chick-rearing stage, (•) compared to that of captive birds throughout the year (thick line) based on the long-term average air temperature at Eelde (53°08'N, 6°35'E) calculated from the relation: *EM* (kJ day^{-1}) = 904 – 30.3 × *T*(°C) (Kersten & Piersma 1987). Also indicated are the maximum amount of energy (1067 kJ day^{-1}) that can be dealt with by the digestive system (Kersten & Visser 1996) and the hypothetical energy expenditure of a leapfrog that provisions the same amount of food to its chick as a resident by increasing its flight time to 4000 s per low water period (Ens *et al.* 1992).

Jacobsen *et al.* 1995) but not in others (review in Dijkstra *et al.* 1990). In most of these studies, parents were assumed to adjust their effort in response to the change in brood size, but this was measured only in the Kestrel *Falco tinnunculus* (Dijkstra *et al.* 1990, Deerenberg *et al.* 1995). When manipulated brood size increased from two to seven chicks, the energy expenditure of the parents increased from 3.4 to 4.5 × *BMR* while their local survival until the next breeding season decreased dramatically from 67% to 22% (Deerenberg *et al.* 1995). This direct link between parental energy expenditure and subsequent survival suggests that there are fitness costs associated with hard work. Leapfrog Oystercatchers do not work that hard during the breeding season, their energy expenditure is on average only 2.7 × *BMR* during the chick-rearing stage. At the same time, their annual survival rate is high. In most years 95% of the breeding adults returned the next season. In the odd years when a severe cold spell intervenes in winter, mass mortality can occur, but even then adult survival was still 80-90% (Hulscher 1989). Consequently Oystercatchers may become very old, individuals older than 20 years are no exception and the oldest bird known aged 44 years (Exo 1993). With such a high life expectancy, it should not come as a surprise that Oystercatchers are reluctant to increase parental effort at the expense of their prospects of survival. At the same time, the low annual mortality will make it very difficult to demonstrate that a trade-off between parental effort and subsequent survival really exists.

Nevertheless, the safety margin maintained by leapfrogs, operating at 2.7 *BMR*, seems quite large. This may indicate that the risk of mortality starts to increase already at a rather low level of parental energy expenditure. It is remarkable that the daily energy expenditure of Oystercatchers in winter is almost certainly well above 2.7 *BMR*, with no apparent ill-effect on their survival in normal years (Fig. 7). So the question arises why an energy expenditure above 2.7 *BMR* during the breeding season should entail an increased risk of mortality whereas the cost of operating at a higher level at other times of the year is easily dealt with as indicated by the high survival rate in normal years. Although admittedly speculative, seasonal changes in the rate of parasite infections through the food may provide a possible way out of this apparent paradox. The risk of contracting such an infection is at least proportional to the amount of food consumed. If an increase in consumption is achieved at the expense of selectivity, infection risk increases even more. Consequently, by operating at a level of 2.7 *BMR* instead of the possible 4 *BMR*, parent Oystercatchers reduce their infection risk by at least one third. Some observations suggest that the infection risk may vary with season indeed. *Macoma balthica* serves both as first and second intermediate host for the trematode *Parvatrema affinis* whose final host is a bird (Swennen & Ching 1974). Infected Macoma rise to the mud surface where they are very conspicuous. When moving, they leave a highly visible trace which reveals there locality even after they have withdrawn into the mud again. This behaviour should make them more vulnerable to predation, but Oystercatchers reject these infected *Macoma* (Hulscher 1981). Traces of infected *Macoma* are very abundant in late spring and early summer but become much scarcer later in the season (pers. obs.), presumably because most infected *Macoma* have died. This would create an annual cycle in the abundance of infected *Macoma*, which is consistent with the observation that the rejection rate of *Macoma* by Oystercatchers decreased from 6.3% in June to 4.4% in August (Hulscher 1981).

ACKNOWLEDGEMENTS

The Oystercatcher study owes much to Jan Hulscher who initiated the marking program in 1983 and kept all birds in the study area individually recognizable ever since. Many students were involved in the continuous observations to construct the time budgets. The most persistent among these were: Dieko Alting, Alex Brenninkmeijer, Arjo Bunskoeke, Bruno Ens, Rinke Hoekstra, Theo Jager, Willem Visser and Sake de Vlas. The big tower on the mudflats was kindly made available by

Kees Swennen of the Netherlands Institute for Sea Research. Jan Koenes, Jan Nijboer and Edzo Paap proved indispensable for the construction and maintenance of all kinds of equipment. The student-proof event-recorders were designed and manufactured by Kees Rappoldt, who also supplied the software to get something meaningful out of the data stored in memory. The Dienst der Domeinen allowed us to work on their property. Berthe Verstappen-Du Moulin performed the isotope analyses. This paper has benefited much from continuous discussions with and suggestions made by Rudi Drent, Bruno Ens, Jan Hulscher, Kees Rappoldt, Joost Tinbergen and Leo Zwarts. This study was supported by BION (Foundation for Biological Research, grant 436.123), itself subsidized by NWO (Netherlands Organization for Scientific Research).

REFERENCES

Askenmo C. 1979. Reproductive effort and return rate of male Pied Flycatchers. Am. Nat. 114: 748-753.

Astheimer L.B. & C.R. Grau 1990. A comparison of yolk growth rates in seabird eggs. Ibis 132: 380-394.

Brody S. 1945. Bioenergetics and growth. Reinhold Publishing Company, New York.

Bryant D.M. & P. Tatner P. 1991. Intraspecies variation in avian energy expenditure: correlates and constraints. Ibis 133: 236-245.

Bunskoeke E.J., B.J. Ens, J.B. Hulscher & S.J. de Vlas 1996. Why do Oystercatchers (*Haematopus ostralegus*) switch from feeding on the Baltic Tellin *Macoma balthica* to feeding on the Ragworm *Nereis diversicolor* during the breeding season? Ardea 84A: 91-104.

Deerenberg C., I. Pen, C. Dijkstra, B. Arkies, G.H. Visser & S. Daan 1995. Parental energy expenditure in relation to manipulated brood size in the European Kestrel *Falco tinnunculus*. Zoology 99: 39-48.

Dijkstra C., A. Bult, S. Bijlsma, S. Daan, T. Meijer & M. Zijlstra 1990. Brood size manipulations in the Kestrel (*Falco tinnunculus*): effects on offspring and parent survival. J. Anim. Ecol. 59: 269-285.

Ens B.J., M. Kersten, A. Brenninkmeijer & J.B. Hulscher 1992. Territory quality, parental effort and reproductive success of Oystercatchers (*Haematopus ostralegus*). J. Anim. Ecol. 61: 703-715.

Ens B.J., F.J. Weissing & R.H. Drent 1995. The despotic distribution and deferred maturity: two sides of the same coin. Am. Natur. 146: 625-650.

Ens B.J., E.J. Bunskoeke, R. Hoekstra, J.B. Hulscher, M. Kersten & S.J. de Vlas 1996. Prey choice and search speed: why simple optimality fails to explain the prey choice of Oystercatchers *Haematopus ostralegus* feeding on *Nereis diversicolor* and *Macoma balthica*. Ardea 84A: 73-90.

Exo K.-M. 1993. Hochstalter eines beringten Austernfischers (*Haematopus ostralegus*): 44 Jahre. Vogelwarte 37: 144.

Goede A.A. 1993. Variation in the energy intake of captive Oystercatchers *Haematopus ostralegus*. Ardea 81: 89-97.

Greenewalt C.H. 1975. The flight of birds. Trans. Amer. Phil. Soc. 65: 1-67.

Hart J.S. & M. Berger 1972. Energetics, water economy and temperature regulation during flight. Proc. XV Int. Ornithol. Congr.: 189-199.

Heyman M.B. & S.B. Roberts 1990. Determination of total energy expenditure in infants using doubly labelled water ($^2H_2{}^{18}O$). In: T.E. Chapman, R. Berger, D.J. Reijngoud & A. Okken (eds) Stable isotopes in paediatric nutritional and metabolic research: 51-66. Intercept, Andover, Hampshire.

Hulscher J.B. 1982. The Oystercatcher *Haematopus ostralegus* as a predator of the bivalve *Macoma balthica* in the Dutch Wadden Sea. Ardea 70: 89-152.

Hulscher J.B. 1985. Growth and abrasion of the oystercatcher bill in relation to dietary switches. Neth. J. Zool. 35: 124-154.

Hulscher J.B. 1989. Sterfte en overleving van Scholeksters *Haematopus ostralegus* bij strenge vorst. Limosa 62: 177-181.

Hüppop O. & K. Hagen 1990. Der Einfluß von Störungen auf Wildtiere am Beispiel der Herzschlagrate brütender Austernfischer (*Haematopus ostralegus*). Vogelwarte 35: 301-310.

Jacobsen K-O., K.E. Erikstad & B-E. Saether 1995. An experimental study of the costs of reproduction in the Kittiwake *Rissa tridactyla*. Ecology 76: 1636-1642.

Janes D.N. & M.A. Chappell 1995. The effect of ration size and body size on specific dynamic action in Adélie Penguin chicks, *Pygoscelis adeliae*. Physiol. Zool. 68: 1029-1044.

Kendeigh S.C. 1974. Untitled. In: R.A. Paynter (ed.) Avian energetics. Nutall Ornith. Club: 70-79. Cambridge, Mass.

Kersten M. & T. Piersma 1987. High levels of energy expenditure in shorebirds: metabolic adaptations to an energetically expensive way of life. Ardea 75: 175-187.

Kersten M. & A. Brenninkmeijer 1995. Growth, fledging success and post-fledging survival of juvenile Oystercatchers *Haematopus ostralegus*. Ibis 137: 396-404.

Kersten M. & W. Visser 1996. Food intake of Oystercatchers *Haematopus ostralegus* by day and by night measured with an electronic nest balance. Ardea 84A: 57-72.

Klaassen M., M. Kersten & B.J. Ens 1990. Energetic requirements for maintenance and premigratory body mass gain of waders wintering in Africa. Ardea 78: 209-220.

Masman D. & M. Klaassen 1987. Energy expenditure during flight in trained and free-living Eurasian Kestrels, *Falco tinnunculus*. Auk 104: 603-616.

Pennycuick C.J. 1975. Mechanics of flight. In: Farner D.S. & King J.R. (eds) Avian Biology, 5: 1-75. Academic Press, London.

Pennycuick C.J. 1989. Bird flight performance, a practical calculation manual. Oxford University Press, Oxford.

Rayner J.M.V. 1979. A new approach to animal flight mechanics. J. Exp. Biol. 80: 17-54.

Rayner J.M.V. 1990. The mechanics of flight and bird migration performance. In: E. Gwinner (ed.) Bird migration, physiology and ecophysiology: 283-299. Springer-Verlag, Berlin.

Reid W.V. 1987. The cost of reproduction in the Glaucous-winged Gull. Oecologia 74: 458-467.

Roudybush T.E., C.R. Grau, M.R. Petersen, D.G. Ainly, K.V. Hirsch, A.P. Gilman & S.M. Patten 1979. Yolk formation in some Charadriiform birds. Condor 81: 293-298.

Speakman J. 1984. The energetics of foraging in wading birds. Ph.D. thesis, University of Stirling, Stirling.

Stearns S.C. 1976. Life-history tactics: a review of the ideas. Q. Rev. Biol. 51: 3-47.

Swennen C. & H.L. Ching 1974. Observations on the trematode *Parvatrema affinis*, causative agent of crawling tracks of *Macoma balthica*. Neth. J. Sea Res. 8: 108-115.

Taylor C.R., N.C. Heglund & G.M.O. Maloiy 1982. Energetics and mechanics of locomotion. I. Metabolic energy consumption as a function of speed and body size in birds and mammals. J. Exp. Biol. 97: 1-21.

Videler J.J. 1995. Consequences of weight on flight performance during migration. Isr. J. Zool. 41: 343-356.

Zwarts L. & J.H. Wanink 1993. How the food supply harvestable by waders in the Wadden Sea depends on the variation in energy density, body weight, biomass, burying depth and behaviour of tidal-flat invertebrates. Neth. J. Sea Res. 31: 441-476.

SAMENVATTING

Scholeksters die direct aan de kwelderrand broeden zijn in het voordeel vergeleken met vogels die dat verder landinwaarts doen, omdat de kwelderrandbroeders een territorium bezitten dat zich uitstrekt over het aangrenzende wad; ze worden daarom hokkers genoemd. De vogels die niet langs de rand broeden, vliegen heen en weer tussen hun voedselgebied op het wad en hun nest; ze worden daarom wippers genoemd. Wippers moeten zich meer inspannen om een jong groot te brengen dan hokkers. Als de jongen moeten worden gevoerd, zijn de wippers tijdens de laagwaterperiode 8.2% van de tijd aan het vliegen tegen 2.9% bij de hokkers. Hokkers zowel als wippers doen een groot deel van de tijd niets: voordat de eieren worden gelegd, wordt 50% van de laagwaterperiode gerust en gepoetst, en zelfs als beide partners elk de helft van de tijd zitten te broeden, wordt nog altijd 23% van de potentiële foerageertijd gerust en gepoetst. Analyse van het tijd budget van verschillende individuen laat zien dat de vogels tijd 'over' hebben, zelfs als er voedsel naar de jongen moet worden gebracht. Het energie budget werd geschat op basis van: (1) het tijdbudget (waarbij voor elke type activiteit een bepaalde energieuitgave werd aangenomen), (2) de voedselopname en (3) zwaar water metingen. De schattingen kwamen overeen. De energieuitgave varieerde tussen 2.1 × basaal metabolisme (BMR) tijdens het broeden tot 2.7 × BMR als ze jongen hebben. Deze waarden zijn veel lager als die gemeten zijn bij veel andere vogelsoorten tijdens de voortplanting. In de jongen-fase geven wippers 6 tot 7% meer energie uit dan de hokkers, als gevolg van de hogere vliegkosten. Wippers brengen minder jongen groot dan hokkers omdat ze minder voer naar hun jongen brengen. Wippers zouden harder kunnen werken, maar ze doen het niet. Scholeksters zijn langlevende vogels. Ze maken blijkbaar de afweging om zich in het broedseizoen niet bovenmatig in te spannen.